PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES
FOURTH SERIES

Festschrift for George Sprague Myers

Vol. XXXVIII, No. 20, pp. 383–390 December 31, 1970

SCALE-EATING AMERICAN CHARACOID FISHES, WITH SPECIAL REFERENCE TO *PROBOLODUS HETEROSTOMUS*

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INTRODUCTION

Specialized scale-eaters have been discovered in three groups of American characoids. Kner (1860, p. 34) reported the stomach of a large specimen of *Catoprion* full of scales and referred to them as "Raubfische." Ladiges, observing this peculiar serrasalmid in an aquarium, saw one remove a row of scales from a specimen of *Metynnis* with one swipe of its teeth (reported by Géry, 1964, p. 460). Breder (1927, p. 127) reported substantial amounts of large scales in stomach contents of representatives of *Roeboides occidentalis* from eastern Panama and identified some of the scales as coming from *Ctenolucius,* a pike-like characoid considerably larger than the specimens of *Roeboides.* Géry (1964, pp. 459–460) reported scale-eating in *Exodon, Roeboides,* and *Roeboexodon,* of the characid subfamily Characinae. In this paper the activity is verified for *Catoprion, Exodon, Roeboexodon,* and two additional species of *Roeboides* and is reported for the first time in *Probolodus heterostomus* Eigenmann,[1] a member of the characid subfamily Tetragonopterinae.

Although Géry supposed that scale-eating occurred in *Catoprion, Exodon, Roeboexodon,* and *Roeboides* only occasionally, in these genera and in *Probolodus* scales are definitely a major item in stomach contents, and eating scales is prob-

[1] Myers (1942, p. 91), in recording specimens from the western end of the coastal plain of Rio, commented on their almost unbelievably strange dentition. The species also occurs in the rios Doce, Paraiba (formerly spelt Parahyba), and Ribeira.

ably a significant factor in the mode of life of these fishes. *Serrasalmus elongatus* includes some scales in its diet but is primarily a fin-eater. Matthes (1961) reported that the African characoids *Phago, Belonophago,* and *Eugnathichthys* (family Ichthyboridae) are fin-eaters. There are reports in the literature on aquarium fishes that the eating of fins and scales occurs in *Phago.* Matthes (1964, pp. 65–66) reported scales in stomach contents of specimens of *Belonophago hutsebouti, Phago boulengeri,* and (1961, p. 79) *Eugnathichthys,* but these fishes are primarily fin-eaters. The only other fresh-water scale-eaters of which I am aware are certain highly specialized African cichlids (see Fryer, Greenwood, and Trewavas, 1955). I have not searched thoroughly for accounts of marine scale-eating fishes. There probably are some; Springer and Woodburn (1960, p. 22) stated that annelids and fish scales (with no other fish remains) constituted the major portion of stomach contents of sea catfish (*Galeichthys felis*) taken in Tampa Bay.

This paper was prepared at the Departamento de Zoologia of the Secretaria da Agricultura in São Paulo during a visit in April and May, 1969. All observations are based on specimens in the Departamento's collections. Measurements of fishes given in mm. refer to standard length.

OBSERVATIONS

Probolodus.

MATERIAL EXAMINED. DZSP 7903, 40 specimens, 41–97 mm., from Rio Paraíba below reprêsa de Santa Branca (state of São Paulo), col. 10–13 February 1962 by H. A. Britski; and DZSP 7904, 92 specimens, 38–71 mm., reprêsa de Santa Branca, Rio Paraíba, collected 10–16 September 1963 by H. A. Britski and J. Rossi.

STOMACH CONTENTS. Stomach contents were examined in 30 specimens ranging from 38 to 97 mm. Twenty of these were from the February, 1962 collection, and 10 from September, 1963. The stomachs contained food in all specimens. Scales were by far the major item encountered and occurred in all but 1 specimen. They were the only item present in about 50 percent. The number of scales in a stomach varied from 3 to 40, with a mean of about a dozen. Most of the scales were 3–5 mm. in diameter, substantially larger than *Probolodus*' own scales. A white substance of loose consistency was present in large quantity in 5 specimens of the February, 1962, sample. Otherwise food items in the 2 samples were very similar. The following items were also encountered: small seeds (1 or 2), in 3 specimens; soil? (small quantities), 3 specimens; minute crustaceans (about 50), 1 specimen; insect larva (1), 1 specimen; hymenopteran (1), 1 specimen. The smallest specimens examined—38, 41, 47, and 49 mm.—have stomach contents similar to the others.

DENTITION. The teeth of *Probolodus* have been described and figured by Eigenmann (1915, pp. 20–21, fig. 5). *Probolodus* has very few teeth and, as in

many other characoids with highly specialized dentition, the number is constant or very nearly so. Basically there are 3 widely separated teeth on each premaxillary and 5 on each dentary. Often a tooth is missing, but this is due to loss or shedding to make way for a replacement tooth. There are usually either 3 or 4 teeth on each maxillary, but as few as 2 or as many as 5 were present on some specimens. Here, too, replacement affects the number present. All of the teeth are strictly tricuspid. The 3 cusps form a triangle with the enlarged median cusp at the anterior angle. The lateral cusps are equal in size and very small. The tooth base is moundlike and stout.

The premaxillary teeth point out of the mouth. The first 3 dentary teeth also point out. Only the fourth and fifth dentary teeth lie inside the mouth. The enlarged fourth dentary tooth is situated internally to the third and slightly posterior to it, and the reduced fifth is directly behind the fourth. (Note.—Eigenmann refers to one *or more* small teeth behind the fourth. In specimens I have examined there is only one. Perhaps the presence of additional teeth in an occasional specimen is a primitive or vestigial character.) The cusps of the anteriormost premaxilliary and dentary teeth point almost straight ahead of the fish. The third dentary tooth, and to a lesser extent the third premaxillary tooth, project laterally from the mouth. The teeth are not juxtaposed but are separated from each other by a gap about equal to the diameter of a tooth base. When the mouth is closed the teeth of the upper and lower jaws interdigitate rather than truly oppose each other. Thus the first dentary tooth occupies the gap between the first and second premaxillary teeth, the second dentary tooth that between second and third premaxillary teeth, and the third dentary tooth that between the third premaxilliary and first maxillary teeth. The fourth and fifth dentary teeth do not oppose or interdigitate with other teeth and neither do the lowermost teeth on the maxillary. One can easily imagine how scales are firmly grasped by such teeth and then dislodged by the kind of tugging movements many characids make when feeding. The number, form, and arrangement of the teeth are the same in specimens from 38 to 97 mm.

Tooth replacement. Twenty specimens from the September, 1963, collection were examined for signs of tooth replacement. In only 2 specimens were all of the premaxilliary and dentary teeth in functional position and firmly attached to the jawbones. In each of the remaining 18 from 1 to 4 teeth were in the process of replacement or had just come into functional position (teeth in the process of replacement can be detected immediately below the gum or making their way through it; teeth that have just come into functional position are recognizable as such because the cusps are unworn and very sharp, the bases are usually surrounded by soft, swollen tissue, and the attachment to the jaw is very loose). The data indicate that replacement occurs more frequently in lower jaw teeth than in upper, and that certain teeth are replaced with relatively high frequency. In all, 40 instances of tooth replacement in process and teeth newly in functional posi-

tion were observed, 29 in the dentary and 11 in the premaxillary. No fewer than 9 instances involve the fourth dentary tooth. At the other extreme, the first premaxillary tooth is involved in only 1 instance. Judging from their appearance the teeth in the lower jaw receive more wear than those in the upper jaw.

Sex. Almost all specimens in the February, 1962, collection have readily identifiable gonads. The others were sexed by the presence (males) or absence of tiny serrations on the anterior anal fin rays. The reliability of this method was checked in specimens in which the sex of the gonads was obvious. Of the 40 specimens in the sample, 29 (72 percent) are females and 11 (28 percent) males. Females range from 40.5 to 97 mm. and average 68 mm., 12 mm. more than the males. Males range from 47 to 65 mm. and average 56 mm. The largest female is 32 mm. longer than the largest male. Combined biomass of females is slightly more than three times that of males. The 40.5 mm. specimen contained about 200 eggs, most .6–.7 mm. in diameter but a few somewhat smaller; a 73.5 mm. specimen contained about 2500, all about .7–.8 mm. in diameter.

Serrasalmus elongatus.

Stomach contents were examined in 7 specimens of *S. elongatus* Kner, 89–152 mm., from 3 Amazonian localities. Pieces of the rayed portion of fins and scales were present in every specimen; they were the only items encountered in 5 of the specimens. In all but 2 fin rays were by far the major item. One specimen had about 50 scales and only a few small bits of fin rays. The 152 mm. specimen (collected in Lago Jacupá, near Oriximiná, state of Pará, in February, 1967) contained 6 cichlid larvae of about 8 mm.; 13 fish? eggs of about 2 mm. in diameter; 2 large pieces of very hard, thick fin rays, perhaps from the caudal fin of a sorubim catfish; and 8 scales about 5–6 mm. in diameter. One specimen, with its stomach moderately full of fin rays and a few scales, had a small matted ball of fibrous plant material including 3 small seeds. All items encountered have been indicated; noteworthy is the absence of pieces of meat. Stomach contents of several *Pygocentrus*-type piranhas have been examined and when scales were encountered there were also bits of meat. Many piranhas feed to some extent on fins. *S. clongatus* is apparently a fin-eater which feeds to a certain extent on scales.

Catoprion.

Kner (1860, p. 34) found the stomach of a large *Catoprion* specimen full of scales. Gosline (1951, p. 54) examined the stomachs of 4 specimens and reported that "two were full of fish scales and two were empty except for a few fish scales; a small amount of unidentifiable debris was also found." Géry (1964, p. 460) found scales in stomachs of specimens from Bolivia. In examining 4 specimens, 103–109 mm., from 3 Amazonian localities I find that their stomachs are more or less full of scales about 6–15 mm. in diameter. The only other items are a few bits of leaf from a higher plant (in 2 specimens) and a small ball of

fibrous plant material, probably roots (in 1 specimen). Scales are thus the only item that has been encountered in substantial amounts in stomachs of *Catoprion*. The teeth in this genus are illustrated by Müller and Troschel (1845, pl. 2, fig. 5).

Exodon.

Géry (1964, p. 459) reported scales in stomach contents of *Exodon* from the Rio Araguaia. I examined 10 specimens, 36–59.5 mm., from the Rio Araguaia at Aruanã and found from 4 to 15 scales, mostly 3–5 mm. in diameter, in every one. The only other item was small amounts of unidentifiable material in 2 specimens. Kner (1860, p. 47) found beetles in 2 specimens from the Rio Branco. The teeth of *Exodon* are figured by Müller and Troschel (1845, pl. 4, fig. 1a).

Roeboexodon.

This genus has hitherto been known only from a few specimens taken in French Guiana (Géry, 1959). In September, 1966 Heraldo A. Britski and P. E. Vanzolini collected 2 specimens (DZSP 4815, 41.5 and 45.5 mm.) from the Rio Araguaia near Aruanã in the Brazilian state of Goiás. The dentition of these specimens is identical with that in an alizarin preparation of a 29 mm. specimen from French Guiana (kindly sent to the Departamento de Zoologia by Géry) and they apparently represent the same species. The stomach contents of both specimens consist exclusively of scales from about 2.5 to 4 mm. in diameter. The 41.5 mm. specimen contained about 10 scales and the 45.5 mm. specimen about 20. The teeth of *Roeboexodon* are described and partially figured by Géry (1959, pp. 347–349, fig. 2).

Roeboides.

Naercio Menezes and I examined stomach contents in 9 specimens of *Roeboides guatemalensis*, 6 of *R. myersi*, and 25 of *R. prognathus*. In all 6 specimens of *R. myersi* (117–160 mm.) and in the 11 largest of *R. prognathus* (70–90 mm.) the stomachs are more or less filled with scales, to the exclusion of all else, those of *R. myersi* with from 15–35 scales mainly 6–9 mm. in diameter and those of *R. prognathus* with 40–150 scales 3–6 mm. in diameter. In 14 smaller examples of *R. prognathus* (41–68 mm.) scales predominate, but insects—Diptera, Hemiptera (Notonectidae?), and a few Coleoptera—occur with high frequency. A 64 mm. specimen contained a fish larva. Our specimens of *R. guatemalensis* (72.5–101 mm., from Gatun Lake, Panama Canal Zone, collected in November, 1965) have viscera heavily infested with nematodes and may not have been feeding normally. The stomachs are empty in 4 of them and the other five contain but little food, as follows: a few scales (in 4); shrimp (in 2); insect (in 1); and an unidentified, flocculent, white material (in 1).

In very small specimens of *Roeboides* (20–30 mm.) the teeth can be recognized

as belonging to *Roeboides* because of their slightly hypertrophied bases, but they are all normal in position. Examination of stomach contents in a few specimens (unidentified to species) indicates that at these sizes they feed primarily on insects. Only at about 30–60 mm., depending on the species, is the transition made to the adult condition in which teeth with greatly hypertrophied bases project from the front of the jaws.

DISCUSSION

Stomach contents of fishes belonging to *Catoprion, Probolodus, Exodon, Roeboides,* and *Roeboexodon* indicate that their diet consists mainly of scales. The teeth are so highly specialized in some of these fishes as to suggest that they could not survive in nature on the food that their non-scale-eating ancestors fed upon. The remarkable "twin spot" color pattern of *Exodon* and relatively small scales of *Probolodus* may have evolved after the scale-eating behavior to reduce intraspecific scale-eating. Breder (1927, p. 127) speculated that the small, thin, and very adherent nature of the scales of *Roeboides occidentalis* reduces autopredation. Whereas *Catoprion, Exodon, Roeboexodon,* and *Probolodus* are monotypic, *Roeboides* has speciated extensively.

The relationships of the five genera, although not yet well understood, show that they represent at least three independent lines of evolution: 1. *Catoprion* is definitely a serrasalmid, and probably descended from *Serrasalmus. Serrasalmus elongatus* includes scales in its diet but is primarily a fin-eater and does not appear to be closely related to *Catoprion.* 2. Eigenmann (1911; 1915) stated that *Probolodus* is very similar in general appearance to *Astyanax fasciatus* but placed it in his polyphyletic subfamily Aphyocharacinae (= Cheirodontinae). In my opinion *Probolodus* belongs in the Tetragonopterinae; it probably descended from *Astyanax.* It is certainly not related to either *Cheirodon* or *Aphyocharax.* 3. *Roeboides* is closely related to *Charax* and *Eucynopotamus.* Géry (1959, pp. 404–405) suggested that *Exodon* was derived from *Holobrycon* and *Roeboexodon* from *Exodon,* and placed *Roeboides* and *Charax* in a different line. Naercio Menezes and I intend to study the osteology of these Characinae in an effort to clarify their relationships. We suspect that *Eucynopotamus,* apparently intermediate between *Charax* and *Roeboides,* is actually based on the young of *Roeboides,* and note that *Roeboexodon* bears a strong superficial resemblance to *Roeboides prognathus* Boulenger.

Perhaps the strange gymnotoid eel *Oedemognathus exodon* Myers is a scale-eater. According to Myers (1936, p. 115), in this apteronotid "the dentigerous portion of the premaxillaries is greatly expanded and bulbous, most of it not opposable to the lower jaw, and the upper part of it rising above the profile of the snout. The whole of this bulbous area is studded with many strong, slightly curved, conical teeth, placed irregularly and not very closely together. Most of the upper teeth therefore project forward, outward or upward, and are entirely

outside the mouth. The lower teeth are similar to the upper ones in shape, and are numerous and arranged irregularly, but none is outside the mouth and all point in normal direction." *Oedemognathus* is known only from the holotype, 202 mm. in total length, USNM 102040, and a 92 mm. specimen reported on and figured by Eigenmann and Allen (1942, pp. 325–326, pl. 15, figs. 2–3), CAS (IUM) 15421, both from the Peruvian Amazon.

ACKNOWLEDGMENTS

I wish to thank Daniel M. Cohen of the U. S. Fish and Wildlife Service and Stanley H. Weitzman of the U. S. National Museum for critical comments on the manuscript.

ADDENDUM

Mr. William A. Bussing of the Departamento de Biologia, Universidad de Costa Rica, informs me that Sr. Carlos Leon, Administrador of the Parque Bolivar in San José, Costa Rica, observing 2 fish in an aquarium, saw one (*Roeboides guatemalensis*) butt the other (*Astyanax* sp.) with its snout and then catch the dislodged scales as they sank. Bussing has examined the viscera of about 100 representatives of *R. guatemalensis* during fieldwork on the Atlantic and Pacific slopes of Costa Rica and found almost every specimen had scales and virtually nothing else in the stomach. A few contained small insect larvae and one a small fish.

At the John G. Shedd Aquarium in Chicago, Mr. Emanuel Ledecky-Janecek, Curator of Exhibits, kindly responded to my request and placed a specimen of *Leporinus* (perhaps *L. friderici*) about 9 or 10 inches long in with a small tankful of fish belonging to *Exodon paradoxus*. Within a few moments we saw the latter agitatedly gang up to one side of the *Leporinus* victim and take turns making extremely rapid circular stabbing motions against its side, always striking towards the free margin of the scales, and removing a single scale at about every other strike. The scales were swallowed directly. On only one occasion did a scale fall to the bottom of the tank and a moment later it too was devoured. In about 5 or 10 minutes 20 or 30 scales had been eaten.

At the Steinhart Aquarium of the California Academy of Sciences I watched several fish belonging to *Leporinus fasciatus* determinedly nipping at fungus-infected sores on a specimen of *Astronotus ocellatus*. I am unsure, but think that the cichlid lost a few scales, although the *Leporinus* specimens seemed to confine their nipping to the sores.

LITERATURE CITED

Breder, Charles M.
1927. The fishes of the Rio Chucunaque drainage, eastern Panama. Bulletin of the American Museum of Natural History, vol. 57, art. 3, pp. 91–176.

Eigenmann, Carl H.

1911. New characins in the collection of the Carnegie Museum. Annals of the Carnegie Museum, Pittsburgh, vol. 8, no. 3, pp. 164–181, pls. 4–9.

1915. The Cheirodontinae, a subfamily of minute characid fishes of South America. Memoirs of the Carnegie Museum, Pittsburgh, vol. 7, no. 1, pp. 1–99, pls. 1–17.

Eigenmann, Carl H., and W. R. Allen

1942. Fishes of western South America. University of Kentucky, pp. i–xv, 1–494, map.

Fryer, Geoffroy, P. H. Greenwood and E. Trewavas

1955. Scale-eating habits of African cichlid fishes. Nature, vol. 175, no. 4468, pp. 1089–90.

Géry, Jacques

1959. Contribution à l'étude des poissons characoïdes (Ostariophysi) (II.) *Roeboexodon* gen. n. de Guyane, redescription de *R. guyanensis* (Puyo, 1948) et relations probables avec les formes voisines. Bulletin du Muséum National d'Histoire Naturelle, second series, vol. 31, no. 4, pp. 345–352; and no. 5, pp. 403–409.

1964. Poissons characoïdes nouveaux ou non signalés de l'ilha do Bananal. Vie et Milieu, suppl. 17 (Volume Jubilaire dédié à Georges Petit), pp. 447–471.

Gosline, William A.

1951. Notes on the characid fishes of the subfamily Serrasalminae. Proceedings of the California Academy of Sciences, fourth series, vol. 27, no. 2, pp. 17–61, pls. 1–3.

Kner, Rudolf

1860. Zur Familie der Characinen, II. Denkschriften der mathematisch-naturwissenschaftlichen Classe der kaiserlichen Akademie der Wissenschaften, Wien, vol. 18, pp. 9–62, pls. 1–8.

Matthes, Hubert

1961. Feeding habits of some central African fishes. Nature, vol. 192, pp. 78–80.

1964. Les poissons du Lac Tumba et de la région d'Ikela. Annales Musée Royale de l'Afrique Centrale, series in octavo, sciences zoologiques, no. 126, pp. 1–204, 2 maps, 1 chart, pls. 1–6.

Müller, Johannes, and F. H. Troschel

1845. Horae Ichthyologicae. I & II, Die Familie der Characinen. Berlin, pp. 1–40, pls. 1–11.

Myers, George S.

1936. A new genus of gymnotid eels from the Peruvian Amazon. Proceedings of the Biological Society of Washington, vol. 49, pp. 115–116.

1942. Studies on South American fresh-water fishes. I. Stanford Ichthyological Bulletin, vol. 2, no. 4, pp. 89–114.

Springer, Victor G., and K. D. Woodburn

1960. An ecological study of the fishes of the Tampa Bay area. Florida State Board of Conservation, Marine Laboratory (St. Petersburg), Professional Papers Series, no. 1, pp. 1–104.